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Avian attendance and foraging at army-ant swarms in the tropical rain forest of Los Tuxtlas, Veracruz, Mexico

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ABSTRACT. Foraging and attendance of birds at army-ant swarm raids were studied in the tropical rain forest of Los Tuxtlas, Mexico. Sixty-eight raiding swarms were intercepted over a four-year period of which 57% were *Eciton burchelli* and 43% *Labidus praedator*. A total of 461 birds (37 species/12 families) were recorded at swarms of *E. burchelli* and 208 birds (34 species/10 families) were recorded at *L. praedator* swarms. The mean number of bird species detected per swarm was 7.2 at *E. burchelli* raids and 5.6 at *L. praedator* raids. Red-throated ant-tanagers (*Habia fuscicauda*) were most frequently seen at the swarms of both army-ant species. Other important species were the golden-crowned warbler (*Basileuterus culicivorus*), the white-breasted wood wren (*Henicorhina leucosticta*) and the Kentucky warbler (*Oporornis formosus*). Swarms of both army-ant species were active year-round. Birds weighing between 20 and 40 g dominated perches closest to the ground and the central zone of the swarms, richest in animal prey. Birds weighing less than 20 g occupied higher perches and tended to forage in more peripheral zones. At Los Tuxtlas raiding swarms of army ants are important in the foraging ecology of 44 bird species, including 12 North American migrants.

RESUMEN. La asistencia y caza de artrópodos por aves en oleadas de hormigas marabunta fué estudiada en la selva tropical lluviosa de Los Tuxtlas, México. Sesenta y ocho oleadas fueron interceptadas durante un periodo de cuatro años. De estas el 57% pertenecían a la especie *Eciton burchelli* y el 43% a *Labidus praedator*. Un total de 461 aves (37 especies/12 familias) se registraron en la oleadas de *E. burchelli* y 208 aves (34 especies/10 familias) se registraron en la oleadas de *L. praedator*. El número medio de especies registrada por oleada fué de 7.2 ± 1.7 para *E. burchelli* y de 5.6 ± 2.1 para *L. praedator*. La especie con el mayor índice de asistencia a las oleadas de ambas especies de hormiga marabunta fué *Habia fuscicauda*. Otras especies importantes fueron *Basileuterus culicivorus*, *Henicorhina leucosticta* y *Oporornis formosus*. Las oleadas de ambas especies de hormigas estuvieron activas en todos los meses del año y la asistencia de las aves a las oleadas es predecible en cada mes. Las aves que pesaron entre 20 y 40 gr dominaron las perchas verticales más cercanas al suelo y la zona central de las oleadas donde existe una mayor concentración de artrópodos. En la selva de Los Tuxtlas las oleadas de hormigas marabunta son un elemento importante en la ecología del forrajeo de 44 especies de aves, incluyendo 12 migratorias de Norte América.

KEY WORDS: army-ants, birds, foraging, Mexico, tropical rain forest.

INTRODUCTION

In Neotropical rain forests, raiding swarms of army-ants (tribe Ecitonini), searching for insect prey in the forest floor litter, flush out arthropods and small vertebrates which become ready prey for parasitic flies, lizards, frogs,

toads, resident birds and migrant birds from North America. Two species of army-ants, *Eciton burchelli* Schneirla 1958 and *Labidus praedator* Rattenmeyer 1963 regularly attract birds. Field reports indicate that swarms of *E. burchelli* are a dependable source of animal food, since they are active raiders almost every day and nearly all day long, whereas swarms of *L. praedator* are rather sporadic in activity and often forage at night or underground attracting fewer bird species (Franks 1982, Willis 1966, 1967, Willis & Oniki 1978).

In South and Central American tropical forests some birds (e.g. the ruddy woodcreeper, *Dendrocincla homochroa*, the immaculate antbird, *Myrmeciza immaculata*, the black-crowned antpitta, *Pittasoma michleri*, the bicolor antbird, *Gymnopithys bicolor*, the ocellated anthrush, *Phaenostictus mcleani*) have become specialized in their association with army-ants and more than 70% of their food is derived from foraging at army-ant swarms (Willis 1966). None of these regular or professional ant-following antbirds occur north of Guatemala, only some tanagers and woodcreepers that may attend the swarms (Willis & Oniki 1978).

Very few quantitative data exist on patterns of avian attendance at army-ant swarms in the Neotropics (Franks 1982, Willis 1966, 1967, Willis & Oniki 1978) and data are fewer still for the northernmost limit of the Neotropical rain forest (Green *et al.* 1984, Hardy 1974, Sutton 1951). We report observations on patterns of bird attendance and activity at 68 army-ant swarms encountered during a four-year period (October 1982 - November 1986) while conducting field work on various aspects of animal ecology at the Los Tuxtlas Biological Station (95° 04' - 95° 09' N/S, 18° 34' - 18° 36' E/W) in the southeastern portion of the Mexican state of Veracruz (Estrada & Coates-Estrada 1983).

METHODS

Study site and background

The 700 ha Los Tuxtlas reserve is a research facility of the Instituto de Biología of the Universidad Nacional Autónoma de México. The dominant vegetation type is tall evergreen rain forest (Miranda & Hernández 1963) at 160-530 m above sea level. The climate is hot and humid, with mean annual temperature of 25°C and precipitation of 4900 mm. Rainfall is seasonal, with a dry season from March to May when mean monthly precipitation is 111.7 ± 11.7 mm compared to 486 ± 87 mm for other months of the year; the rainiest months are usually September and October (Figure 1) (for further details see Estrada *et al.* 1985). Litter fall is inversely related to the seasonality of rainfall and arthropod abundance in the litter varies, being highest (400 to 1200 individuals per m²) between January and May and significantly lower in other months (≤ 90 individuals per m²) (Figure 1; García-Aldrete 1986).

At Los Tuxtlas, five species of army-ants (*Eciton burchelli*, *E. hamatum*, *E. mexicanum*, *Labidus praedator* and *Neivamyrmex sumichrasti*) have been docu-

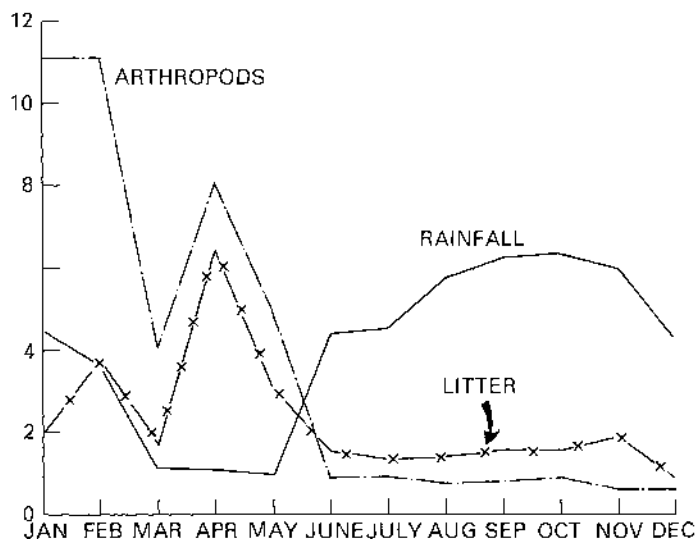


Figure 1. Monthly distribution of rainfall ($N \times 100$ m), litter fall ($g\ m^{-2}\ day^{-1}$) and litter arthropods (individuals m^{-2} ; $N \times 100$) at Los Tuxtlas.

mented (P. Ward personal communication) and 315 species of birds have been identified of which North American migrants (some species present during ten months of the year) comprise 34% of the species (Coates-Estrada *et al.* 1985). Mist-netting and visual censuses of forest understorey birds indicate that the most abundant species are the red-throated ant-tanager (*Habia fuscicauda*), the white-breasted wood-wren (*Henicorhina leucosticta*), the golden-crowned warbler (*Basileuterus culicivorus*) and the following North American migrants: the wood thrush (*Hylocichla mustelina*), the Kentucky warbler (*Oporornis formosus*) and the hooded warbler (*Wilsonia citrina*) (Coates-Estrada & Estrada, unpublished data).

Attendance by birds

Each time an active army-ant swarm was encountered within our study plot (120 ha; elevation 160–200 m) we observed bird attendance for 60 minutes and recorded the following: vegetation type (primary forest, secondary successional growth, forest edge), date, location, time of day, number of individuals of each bird species present and whether or not birds preyed upon organisms flushed by the ants. Perching heights over the swarm area were recorded for each individual bird and grouped for analysis into six height classes from 10.0 cm above ground level to 3.0 m. We recorded the horizontal location of the birds using the division of avian foraging zones around army-ant swarms employed by Willis & Oniki (1978) in Panama: a central zone richest in animal prey and the surrounding middle and peripheral zones with lower concentrations of fleeing animal prey. During the last year of observation, intraspecific and interspecific displacements and chases were recorded for birds occupying the central

zone. A sample of the ants from each swarm was collected and preserved in 70% alcohol for later taxonomic identification.

From mist-net captures an average body weight in grams was assigned to each bird species. Birds were grouped into four weight classes with values ranging from 8 g to >60 g. To determine the regularity of attendance for each bird species observed at the army-ant swarms two measures were used: (1) the proportion of individuals of a particular species with respect to the total number of individuals scored attending the swarms and (2) the frequency of occurrence of a particular species at the swarms intercepted.

Ant swarms

The raiding swarms (N=68) intercepted were determined to belong to two army-ant species: *E. burchelli* (57%), and *L. praedator* (43%). Thirteen raids were without attending birds; nine were *L. praedator*, and the remaining four were *E. burchelli*.

Records of raiding swarms of *E. burchelli* and *L. praedator* were obtained for 11 and nine months respectively of the annual cycle. Swarms were intercepted between 0630 and 1703 h with 79% recorded between 0900 and 1500 h. Interceptions were more common in primary forest, 87% for *E. burchelli* and 69% for *L. praedator*. Forest edge interceptions were 10% and 24% for *E. burchelli* and *L. praedator* respectively. In secondary successional vegetation (5-10 years old) interceptions were only 3% and 7% for swarms of both army-ant species respectively.

Bird attendance

A total of 461 birds representing 37 species and 12 families were recorded attending *E. burchelli* swarms while attendance by 208 birds of 34 species and 10 families was recorded at *L. praedator* swarms. Of the total bird species recorded 66% (N=44) were present at the swarms of both army-ant species. Swarms of *E. burchelli* and *L. praedator* attracted 12 and 10 North American migrant species respectively (Table 1). The mean (\pm SD) number of bird species per swarm at *E. burchelli* raids was 7.2 ± 1.7 (range 2-11) and the mean (\pm SD) number of North American migrants was 1.9 ± 1.3 . (range 1-4). For *L. praedator* raids the mean (\pm SD) number of species attending a swarm was 5.6 ± 2.1 (range 2-10) and the mean (\pm SD) number of North American migrants was 1.6 ± 1.5 (range 1-5).

The bird species with the highest values for the two measures of regularity of attendance at swarms of both army-ant species was *Habia fuscicauda*; all other species had significantly lower values both for the proportion of individuals attending and for frequency of occurrence at swarms (Table 1). The most important species in this latter case for *E. burchelli* swarms were *Basiluterus culicivorus*, the gray-headed tanager (*Eucometis penicillata*), *Henicorhina leucosticta* and *Oporornis formosus*. For *L. praedator* swarms, *B. culicivorus*, the band-backed wren (*Campylorhynchus zonatus*), *H. leucosticta* and *O. formosus* were the most important attendees (Table 1).

Table 1. Bird species observed attending raiding swarms of army-ants at Los Tuxtlas, Mexico. (Names after A.O.U 1983.)

Species	<i>Eciton burchelli</i>					<i>Labidus praedator</i>					
	Indi- vidu- als	%	f (%)	No. of swarms	No. of months	Indi- vidu- als	%	f (%)	No. of swarms	No. of months	Weight g
<i>Habia fuscicauda</i>	152	33	100	35	11	56	27	70	14	8	40
<i>Basileuterus culicivorus</i>	48	10	57	20	10	17	8	30	6	5	10
<i>Eucometis penicillata</i>	41	9	60	21	10	4	2	10	2	2	34
<i>Henicorhina leucosticta</i>	26	6	57	20	8	9	4	35	7	6	16
<i>Hylophilus ochraceiceps</i>	19	4	26	9	7	8	4	20	4	3	11
<i>Attila spadiceus</i>	17	4	37	13	7	7	3	25	5	4	40
<i>Oporornis formosus</i>	16	3	46	16	8	8	4	40	8	3	13
<i>Sittasomus griseicapillus</i>	13	3	20	7	6	5	2	15	3	3	15
<i>Hylocichla mustelina</i>	12	3	34	12	6	5	2	25	5	3	43
<i>Wilsonia citrina</i>	11	2	31	11	7	4	2	20	4	2	10
<i>Habia rubica</i>	10	2	9	3	3	13	6	20	4	3	38
<i>Xiphorhynchus flavigaster</i>	10	2	29	10	9	1	0	5	1	1	60
<i>Helmitheros vermivorus</i>	8	2	23	8	6	4	2	20	4	4	13
<i>Rhynchocyclus brevirostris</i>	8	2	33	8	6	2	1	10	2	2	23
<i>Dendrocicla anabatina</i>	7	2	20	7	6	6	3	30	6	4	42
<i>Dendrocolaptes certhia</i>	7	2	20	7	4	3	1	15	3	3	80
<i>Lepidocolaptes souleyette</i>	7	2	20	7	6	3	1	15	3	3	26
<i>Hylophilus decurtatus</i>	6	1	9	3	3	2	1	5	1	1	10
<i>Catharus ustulatus</i>	5	1	14	5	5	2	1	10	2	2	28
<i>Seiurus aurocapillus</i>	5	1	14	5	5	1	0	5	1	1	17
<i>Thrythorus maculipectus</i>	5	1	9	3	3	3	1	10	2	2	17
<i>Mniotilta varia</i>	4	1	11	4	3	2	1	10	2	2	11
<i>Crotophaga sulcirostris</i>	3	1	3	1	1	3	1	3	1	1	80
<i>Automolus ochrolaemus</i>	2	0	6	2	1	0	0	0	0	0	40
<i>Dendroica magnolia</i>	2	0	3	1	1	0	0	0	0	0	8
<i>Dendroica virens</i>	2	0	6	2	2	3	1	10	2	2	9
<i>Empidonax flaviventris</i>	2	0	6	2	1	2	1	10	2	2	10
<i>Glaucidium brasilianum</i>	2	0	6	2	2	0	0	0	0	0	75
<i>Platyrinchus cancrominus</i>	2	0	6	2	1	0	0	0	0	0	9
<i>Wilsonia canadensis</i>	2	0	3	1	1	4	2	15	3	2	10
<i>Grallaria guatemalensis</i>	1	0	3	1	1	0	0	0	0	0	100
<i>Momotus momota</i>	1	0	3	1	1	0	0	0	0	0	105
<i>Mionectes oleagineus</i>	1	0	3	1	1	0	0	0	0	0	13
<i>Micrastur ruficollis</i>	1	0	3	1	1	1	0	5	1	1	150
<i>Thamnophilus doliatius</i>	1	0	3	1	1	0	0	0	0	0	26
<i>Turdus grayi</i>	1	0	3	1	1	0	0	0	0	0	75
<i>Vireo olivaceus</i>	1	0	3	1	1	0	0	0	0	0	15
<i>Buteo nitidus</i>	0	0	0	0	0	2	1	10	2	1	400
<i>Campylorhynchus zonatus</i>	0	0	0	0	0	18	9	20	4	3	26
<i>Melanerpes aurifrons</i>	0	0	0	0	0	4	2	20	4	1	65
<i>Myiobius sulphureiceps</i>	0	0	0	0	0	1	0	5	1	1	16
<i>Myadestes unicolor</i>	0	0	0	0	0	1	0	5	1	1	35
<i>Piaya cayana</i>	0	0	0	0	0	3	1	15	3	2	110
<i>Turdus assimilis</i>	0	0	0	0	0	1	0	5	1	1	80
Total	461					208					

f (%): frequency of occurrence in swarms.

In 30 cases, birds captured *Anolis* and *Sceloporus* lizards, some of which were foraging on insects flushed by the raiding ants. These records were distributed as follows for each of the involved species: the bright-rumped attila (*Attila spadiceus*) (40%), barred woodcreeper (*Dendrocolaptes certhia*) (27%),

ivory-billed woodcreeper (*Xiphorhynchus flavigaster*) (20%), barred forest-falcon (*Micrastur ruficollis*) (7%), turquoise-browed motmot (*Momotus momotus*) (3%), and squirrel cuckoo (*Piaya cayana*) (3%). The gray hawk (*Buteo nitidus*) and the golden-fronted woodpecker (*Melanerpes aurifrons*) were recorded at the swarms but did not forage on any prey items flushed by the army-ants.

Seasonal differences

The number of swarms intercepted per month ranged from 1 to 7 for *E. burchelli* and from 1 to 5 for *L. praedator*. We found that birds attended swarms in all months for which we recorded swarms. The number of birds recorded attending swarms of *E. burchelli* per month ranged from 14 to 87 and the number of species ranged from 7 to 19. For *L. praedator* swarms the number of individuals ranged from 6 to 52 and the number of species ranged from 4 to 20 (Figure 2).

One species, *Habia fuscicauda*, was observed in all months (N=11) at *E. burchelli* swarms. Its attendance at *L. praedator* swarms was recorded in eight of the nine months documented. At *E. burchelli* swarms, the other birds were observed as follows: five species were seen in eight or more months, nine species occurred in six to seven months, two species occurred in five months and the remainder occurred in less than five months of the annual cycle. For *L. praedator* swarms, only two species occurred in five to six months, all others occurred in less than five months (Table 1).

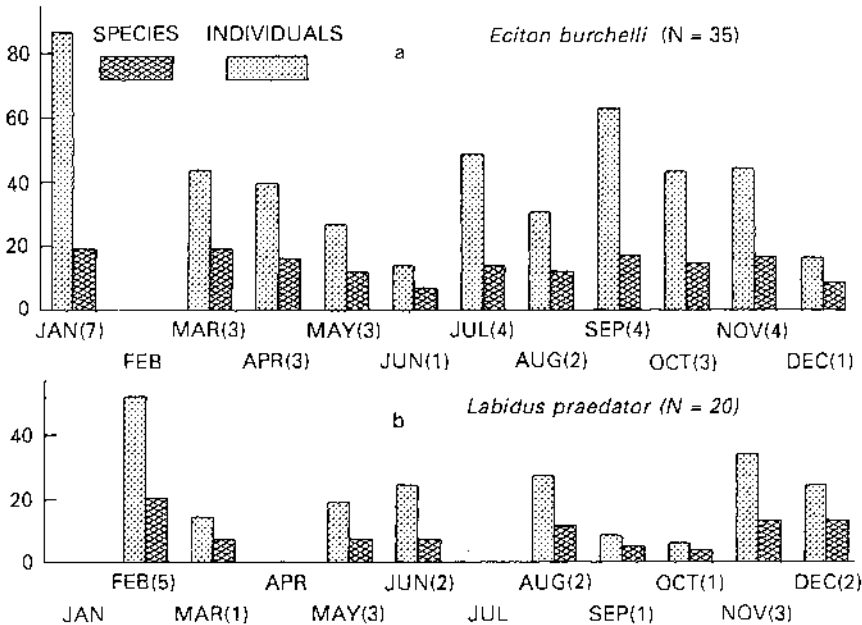


Figure 2. Monthly attendance by birds at raiding swarms of army-ants. Indicated after each month's label is the number of swarms intercepted by us.

Table 2. Distribution of birds in three foraging zones of raiding swarms of *E. burchelli* and *L. praedator*.

	Foraging zones		
	Centre	Middle	Periphery
	<i>Eciton burchelli</i>		
Species	2	19	26
Individuals	164	130	166
NA migrant species	0	4	12
NA migrant individuals	0	16	53
	<i>Labidus praedator</i>		
Species	7	20	20
Individuals	91	69	48
NA migrant species	0	5	9
NA migrant individuals	0	19	16

NA North American.

Foraging zones

Birds foraging at army-ant swarms made sallies from perches to capture flushed prey on the ground, in the air or from the vegetation. Foraging bouts of 5–15 s duration were alternated with brief periods of perching.

The central zone of both species of army-ant swarms contained the greatest number of individual birds but comprised only a few species (Table 2). Only *Habia fuscicauda* (93% of individuals recorded) and *Attila spadiceus* occupied the centre zone at *E. burchelli* swarms. At *L. praedator* swarms, *H. fuscicauda* (63% of individuals recorded), *Campylorhynchus zonatus* and the red-crowned ant-tanager (*H. rubica*) were recorded in this zone. The number of bird species in the middle and peripheral zones was significantly higher than in the centre zone for both species of army-ant swarms (*E. burchelli* $\chi^2=19.4$, $P<0.01$; *L. praedator* $\chi^2=6.5$, $P<0.05$). At six swarms of *L. praedator* in which *H. fuscicauda* was absent the centre zone was occupied by *C. zonatus* followed by *H. rubica*. Noteworthy was the complete absence of North American migrants in the centre zone; they only occurred in the middle and periphery at swarms of both army-ant species (Table 2).

Perch heights

Perches from which birds flew to catch fleeing prey ranged from 0.10 to 3.0 m high at swarms of both army-ant species. More individuals were recorded between 10.0 cm and 0.60 m above ground level than in any other height class and the greatest variety of species occurred between 0.61 and 1.80 m (Table 3); the frequency distribution of species and of individuals occurring at each height class was non random: *E. burchelli* $\chi^2=37.69$, $P<0.01$; *L. praedator* $\chi^2=13.08$, $P<0.02$.

Table 3. Occurrence of birds at each perch height class at raiding swarms of army-ants.

Height class (m)	<i>Eciton burchelli</i>		<i>Labidus praedator</i>	
	Species	Individuals	Species	Individuals
2.41-3.00	5	9	4	6
1.81-2.40	10	23	9	16
1.21-1.80	23	119	16	37
0.61-1.20	28	119	23	54
0.10-0.60	17	191	14	94

Table 4. Frequency of bird species and of individuals in each weight class at raiding swarms of army-ants.

Class (g)	<i>Eciton burchelli</i>		<i>Labidus praedator</i>	
	Number of species	Number of individuals	Number of species	Number of individuals
8-20	18	173	15	73
21-40	8	226	8	99
41-60	4	46	4	19
>60	7	16	5	11

Bird's body weight

The greatest variety of bird species diversity was found in the lowest weight interval (8-20 g) and the greatest number of individuals occurred in the 21-40 g class at swarms of both species of army-ants (Table 4).

The central foraging zone near both species of army-ant was occupied predominantly by birds in the 31-40 g weight class. Individuals of the 8-20 g weight class were most common in the periphery at *E. burchelli* swarms and in the middle and peripheral zones at *L. praedator* swarms. A few species weighing <20 g were present in the centre zone of *L. praedator* swarms, but only when the 31-40 g weight class was absent. Birds with a body weight >40 g occurred principally in the middle zone (Figure 3). Low perches were mostly occupied by birds weighing >20 g, whereas species weighing <20 g were restricted to higher perches (>15 m) (Table 5).

Displacements

Successful intra- or inter-specific displacements or chases away from the centre zones of swarms of *E. burchelli* and *L. praedator* were observed on 64 and 13 occasions respectively. At both species of army-ant swarms *Habia fuscicauda* actively displaced other birds (70% of records) and received only 18% of the displacements. Of the successful displacements made by *H. fuscicauda* 65% were directed at species such as *H. mustelina*, *O. formosus* and *W. citrina* and six others; the remainder were directed toward conspecifics. No correlation was found between displacements received and the birds' body weight (*E. burchelli*, $r = -0.03$ ns; *L. praedator*, $r = -0.428$).

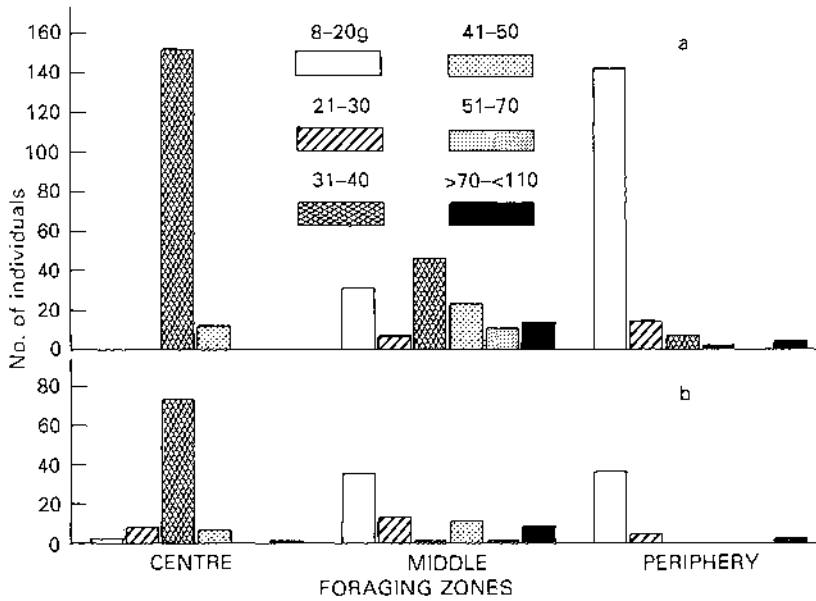


Figure 3. Number of individuals of various weight classes attending each of the foraging zones at raiding army-ant swarms (a: *Ectophasia burchelli*, b: *Labidus praedator*).

Table 5. Distribution of birds within each weight class at each perching height interval.

Height interval (m)	Weight class (g)			
	8-20	21-40	41-60	>60
<i>E. burchelli</i> swarms				
>2.40	6	2	0	2
1.81-2.40	2	1	0	8
1.20-1.80	147	25	18	13
0.61-1.20	18	75	0	20
0.00-0.60	53	123	131	1
<i>L. praedator</i> swarms				
>2.40	5	0	0	1
1.81-2.40	8	1	0	7
1.20-1.80	23	10	3	1
0.61-1.20	15	23	8	8
0.00-0.60	21	72	1	0

Multi-species flocks

Wandering multi-species bird flocks joined foraging birds in 66% and 45% of the records for *E. burchelli* and *L. praedator* swarms respectively. The mean number of species in these flocks were 3.26 ± 0.92 (range 3-6) for *E. burchelli* swarms and 3.44 ± 1.13 (range 2-5) for *L. praedator* swarms. Birds in these flocks such as *Basileuterus culicivorus*, the tawny-crowned greenlet (*Hylophilus ochraceiceps*), and the olivaceous woodcreeper (*Sittasomus griseicapillus*)

weighed < 20 g and perched higher (≥ 1.50 m) than other swarm participants. These flocks generally wandered away after several minutes of foraging (range 4-15 min; $\bar{x} = 8.1 \pm 2.9$) at the peripheral zone of the swarm.

DISCUSSION

The persistent attendance by birds of 44 species including 12 North American migrants at army-ant swarms at Los Tuxtlas suggests that prey fleeing raiding ant swarms are an important food supply; following ants to catch fleeing prey may be less costly than searching the forest floor or low foliage for the same prey items. Several species of reptiles and amphibians inhabiting the forest floor also carry out opportunistic feeding at passing ant raids. Raptors benefit from ant swarms, obtaining large arthropods, reptiles and amphibians and small birds, either because these flee the ants or because they attend the swarms to feed (Franks 1982, Mays 1985). Even multi-species bird flocks moving through the area are attracted to raiding swarms and forage on fleeing prey (Willis & Oniki 1978).

The vertical and horizontal spatial arrangements displayed by birds at the raiding swarms, apparently related to body weight, may allow various species to forage together at this food source. Foraging at army-ant swarms, however, has certain costs for birds that regularly attend the swarms: (1) the swarms' daily changes in raiding routes and in activity rhythms (Franks & Fletcher 1983, Franks & Bossert 1983) may cause birds to invest time and energy in searching for them and (2) the area covered by the slow moving raiding swarm is small (about 10 m^2) creating a tightly packed concentration of potential food for birds and other vertebrates which are forced to compete for direct access to it. Further, the central zone of the swarm, with most fleeing animal prey, may be an even more limited resource to many birds as suggested by the displacement episodes observed; these reflect attempts made by individual birds to enter the richest food patch and attempts to monopolize such a patch within the swarm.

The pre-eminent attendance of *Habia fuscicauda* at raiding swarms of both army-ant species is noteworthy. This forest understorey bird with an average weight of 40 g, lives in family groups of three to five individuals, and is an eclectic feeder consuming insects and fruit throughout the year (Willis 1960, R.C.E. and A.E unpublished data). Whenever an army-ant swarm passed through a group's territory (about 4.5 ha in size) the group joined the raiding swarm with noisy vocalizations and foraged intensely. Its successful access to the richest foraging zone (i.e. the centre) may be the result of its tendency to mob and form coalitions with relatives to displace other birds.

A notable feature of the data is the remarkable consistency in the patterns of attendance by birds at swarms of both army-ant species. A similar number of bird species was recorded at the swarms of *E. burchelli* and *L. praedator*. Attendance at the swarms of both army-ant species was strongly dominated by

Habia fuscicauda. Attendance by *H. fuscicauda*, *Basileuterus culicivorus*, *Henicorhina leucosticta* and *Oporornis formosus* was consistent in time and space and consistent with the dominance of these species in the understory bird community at Los Tuxtlas (A. Estrada, unpublished data). Swarms of both army-ant species are active all year round and bird attendance is predictable throughout the year at raiding swarms. Competition among birds for access to the central foraging zone is persistent at raiding swarms of both army-ant species.

Studies at other Neotropical forest sites show that army-ant colonies require 30 ha or more of forest to meet their energetic demands (Franks 1982). Studies of tropical rain forest fragmentation in Amazonia (Lovejoy *et al.* 1986) indicate that these ants and the associated specialized avian followers are among the organisms that first disappear as the forest is cut. Many bird species recorded attending the swarms are important seed dispersal agents for several plant species at Los Tuxtlas; see Coates-Estrada & Estrada 1986, 1988, Estrada *et al.* 1984). In Mexico tropical rain forests are being destroyed at a rate of 4000 ha year⁻¹ (Estrada & Coates-Estrada 1988) producing an extensive state of fragmentation resulting in a significant depletion of colonies of *Eciton* and *Labidus*. The disappearance of these ants and of their contribution to the sustaining of important ecological links through the potential food they make available to many understory vertebrates is an important conservation problem and will seriously hamper our understanding of the ecological role played by army-ants as 'keystone' organisms at the northernmost limit of the tropical rain forest in the Neotropics.

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LITERATURE CITED

- A.O.U. 1983. *American Ornithologists' Union Checklist of North American Birds*. 6th edition. Allen Press, Inc., Lawrence, Kansas. 877 pp.
- COATES-ESTRADA, R. & ESTRADA, A. 1986. Fruiting and frugivores at a strangler fig in the tropical rain forest of Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 2:349-357.
- COATES-ESTRADA, R. & ESTRADA, A. 1988. Frugivory and seed dispersal in *Cymbopetalum baillonii* (Annonaceae) at Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 4:157-171.
- COATES-ESTRADA, R., ESTRADA, A., PASHLEY, D. & BARROW, W. 1985. *Lista de las Aves de la Estacion de Biología Los Tuxtlas*. Instituto de Biología, Dirección General de Publicaciones de la Universidad Nacional Autónoma de México, México, D.F. 41 pp.
- ESTRADA, A. & COATES-ESTRADA, R. 1983. Rain forest in Mexico: research and conservation at Los Tuxtlas. *Oryx* 17:201-204.

- ESTRADA, A. & COATES-ESTRADA, R. 1988. Tropical rain forest conversion and perspectives in the conservation of wild primates (*Alouatta* and *Ateles*) in Mexico. *American Journal of Primatology* 14:315-327.
- ESTRADA, A., COATES-ESTRADA, R. & MARTINEZ-RAMOS, M. 1985. La Estacion de Biologia Tropical 'Los Tuxtlas': un recurso para el estudio y conservacion de las selvas del tropico humedo. Pp. 379-399 in Gomez-Pompa, A. & del Amo, S. (eds). *Investigaciones sobre la regeneracion de selvas altas en Veracruz, Mexico*. Instituto Nacional Sobre Recursos Bioticos. Editorial Alhambra Mexicana, S.A. de C.V., Mexico. D.F. 421 pp.
- ESTRADA, A., COATES-ESTRADA, R. & VAZQUEZ-YANES, C. 1984. Observations on fruiting and dispersers of *Cecropia obtusifolia* at Los Tuxtlas, Mexico. *Biotropica* 16:315-318.
- FRANKS, N. 1982. Ecology and population regulation in the army ant *Eciton burchelli*. Pp. 389-395 in Leigh, E. G. Jr, Rand, S. & Windsor, D. W. (eds). *The ecology of a tropical forest*. Smithsonian Institution Press, Washington, D.C.
- FRANKS, N. & BOSSERT, W. 1983. Swarm raiding army ants and the patchiness and diversity of a tropical leaf litter ant community. Pp. 151-163 in Sutton, S. L., Chadwick, A. C. & Whitmore, T. C. (eds). *The tropical rain forest*. Blackwell Scientific Publications, Oxford, England.
- FRANKS, N. & FLETCHER, C. 1983. Spatial patterns in army ant foraging and migration: *Eciton burchelli* on Barro Colorado Island, Panama. *Behavioural Ecology and Sociobiology* 12:261-270.
- GARCIA-ALDRETE, A. 1986. Fluctuaciones estacionales de los artrópodos de la hojarasca de la selva alta perennifolia en Los Tuxtlas, Veracruz. *Abstract*. XXI National Congress of Entomology, Monterrey, Mexico.
- GREEN, E., WILCOVE, D. & McFARLAND, M. 1984. Observations on birds at an army ant swarm in Guerrero, Mexico. *Condor* 86:92-93.
- HARDY, J. W. 1974. Jays as army ant followers. *Condor* 76:102-103.
- LOVEJOY, T. E., BIERREGAARD, R. O., RYLANDS, A. B., MALCOLM, J. R., QUINTELA, C. E., HARPER, L. H., BROWN, K. S., POWELL, A. H., LOWELL, G. V. N., SCHUBART, H. O. R. & HAYS, M. B. 1986. Edge and other effects of isolation on Amazon forest fragments. Pp. 57-289 in Soule, M. E. (ed.). *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Inc., Sunderland, Mass. 584 pp.
- MIRANDA, F. & HERNANDEZ, E. 1963. Los tipos de vegetacion de Mexico y su clasificacion. *Bol. Soc. Bot. Mex.* 29:29-129.
- MAYS, N. M. 1985. Ants and the foraging behavior of the collared forest-falcon. *Wilson Bull.* 97:231-232.
- SUTTON, M. G. 1951. Birds and an ant army in southern Tamaulipas. *Condor* 53:16-18.
- WILLIS, E. O. 1960. A study of the foraging behavior of two species of ant tanagers. *Auk* 77:151-170.
- WILLIS, E. O. 1966. The role of migrant birds at swarms of army ants. *Living Bird* 5:187-231.
- WILLIS, E. O. 1967. The behavior of bicolored antbirds. *University of California Publications in Zoology* 79:1-127.
- WILLIS, E. O. & Y. ONIKI. 1978. Birds and army ants. *Annual Review of Ecology & Systematics* 9:243-264.

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